

Herbivory by *Boreioglycaspis melaleucae* (Hemiptera: Psyllidae) Accelerates Foliar Senescence and Abscission in the Invasive Tree *Melaleuca quinquenervia*

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ABSTRACT We quantified the density-dependent effects of herbivory by the psyllid *Boreioglycaspis melaleucae* Moore on the senescence of expanding and fully expanded leaves from two chemical variants (chemotypes) of the invasive tree *Melaleuca quinquenervia* (Cav.) S. T. Blake. Foliar chlorophyll content (OD) and percent nitrogen were not influenced by leaf age classes and chemotypes. In contrast, increases in the level of herbivory resulted in concomitant decreases in chlorophyll compared with undamaged leaves, with medium and high levels of herbivory reducing chlorophyll content by 64 and 72%, respectively. Likewise, low, medium, and high levels of herbivory resulted in 20, 53, and 60% reductions in percent nitrogen, respectively. Color analysis showed that increased herbivory also increased the amount of damaged tissue per leaf across both age classes, but younger leaves showed less susceptibility to herbivory than older leaves. Leaves sustaining moderate to high levels of herbivory progressed from dark green to yellow and finally to light tan as they deteriorated. These changes in color, particularly the yellowing aspect, were often more pronounced along the main leaf veins and vascular tissues. Feeding by *B. melaleucae* increased the likelihood of leaf abscission by 4.7-fold compared with leaves not subjected to herbivory and was not influenced by leaf age or chemotype. Implications for biological control of *M. quinquenervia* are discussed.

KEY WORDS *Melaleuca* psyllid, plant–insect interactions, defoliation, weed biological control, Florida Everglades

The Australian tree *Melaleuca quinquenervia* (Cav.) S. T. Blake (Myrtaceae) was introduced into south Florida by horticulturists during the late 1800s. Nearly 100 yr after its introduction, *M. quinquenervia* was widely recognized as a pernicious invader of wetland systems in the Florida Everglades (Browder and Schroeder 1981, Mazzotti et al. 1981, Woodall 1981, 1982), caused in part by the tree's competitive superiority over most native vegetation (Turner et al. 1998, Dray 2003). Over the past century, *M. quinquenervia* invasion rates have averaged 2,850 ha/yr or ≈ 7.8 ha/d (Laroche and Ferriter 1992, Center et al. 2000). Current estimates of geographic distribution suggest that the invasive tree now occupies $\approx 200,000$ ha of graminoid/herbaceous wetlands, including portions of the Everglades National Park (Turner et al. 1998). These dense *M. quinquenervia* wetland forests are typically composed of up to 132,000 saplings and trees/ha and are characterized by continuous upper canopies with sparse understory vegetation (Rayamajhi et al. 2002). Transitional stages of the invasion include savannahs

with scattered, individual trees, and mature dense stands surrounded by relatively pristine marshes that contain moderate to low levels of the tree (O'Hare and Dalrymple 1997).

A classical weed biological control program targeting *M. quinquenervia* was initiated in 1986, with expectations that introduced herbivores would limit invasion and provide a useful adjunct to conventional control tactics (Balciunas et al. 1994). Surveys for natural enemies of *M. quinquenervia* in eastern Australia reported >450 associated herbivorous arthropod species (Burrows and Balciunas 1999). The curculionid weevil *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) was the first candidate selected for quarantine-based host specificity testing (Purcell and Balciunas 1994) and, once deemed environmentally safe, was released in south Florida in 1997 (Center et al. 2000, Pratt et al. 2003). Feeding by the weevil markedly reduces the tree's reproductive potential (Pratt et al. 2005), but *O. vitiosa* pupates in the soil, so it is unable to thrive in permanently flooded habitats where some *M. quinquenervia* stands persist. To enhance landscape-level suppression of *M. quinquenervia*, a second biological control agent, the psyllid *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae), was released in south Florida during the spring

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of 2002 (Pratt et al. 2004b). By completing its life cycle entirely on the plant, *B. melaleucæ* is less vulnerable to hydrological conditions, and it exploits a wider range of leaf ages than the weevil (Wineriter et al. 2003). Like all psyllids, *B. melaleucæ* passes through five instars (Hodkinson 1974), and development from egg to adult spans 28–40 d (Purcell et al. 1997). First instars are active, but later stages are more sessile and congregate on leaves or stems, secreting copious amounts of white, waxy filaments from dorsal glands (Pratt et al. 2004b). Adults and nymphs feed by inserting their stylets through stomatal pores to gain access to the phloem (Woodburn and Lewis 1973, Purcell et al. 1997).

A fundamental assumption of classical weed biological control asserts that the reunion of natural enemies with their coevolved hosts will reduce plant fitness and limit competitive superiority of the invasive species (McEvoy and Rudd 1993). While host suppression has been documented in other psyllid systems (Hodkinson 1974, Hodkinson 1988, Brennan and Weinbaum 2001), the effect of *B. melaleucæ* on the growth and development of *M. quinquenervia* remains unclear. As one in a series of assessments of *B. melaleucæ*, we studied the density-dependent effect of herbivory on *M. quinquenervia* at the scale of individual leaves. Feeding by *B. melaleucæ* was noted to cause discoloration and ultimately abscission of leaves during quarantine testing conducted before its release (Wineriter et al. 2003). Consistent with laboratory results, preliminary field-based observations of herbivory by *B. melaleucæ* on mature, fully expanded *M. quinquenervia* leaves were often correlated with aseasonal autumnal-like leaf coloration and premature leaf abscission. However, younger expanding leaves near the foliar meristem appeared less susceptible under similar levels of herbivory. In addition, two chemical variants or chemotypes of *M. quinquenervia* occur in Florida (Wheeler and Ordung 2005). The chemotype of *M. quinquenervia* trees is distinguished by the predominate sequesterpene found in its leaves, either *E*-nerolidol or viridiflorol (Wheeler 2005). Recent evidence suggests that *B. melaleucæ* preferentially oviposits on the viridiflorol type over *E*-nerolidol, but development rate and survivorship are not influenced by chemotype (Wheeler and Ordung 2005). Therefore, we sought to determine if herbivory by *B. melaleucæ*, leaf age, and chemotype influenced longevity, color, tissue nitrogen content, and chlorophyll content of *M. quinquenervia* leaves.

Materials and Methods

Melaleuca quinquenervia trees used in this study were vegetatively propagated in 3.8-liters pots during June 2002 using cuttings from stock plants. The chemotype of each sapling was determined (*E*-nerolidol or viridiflorol) by gas chromatography/mass spectroscopy as described by Wheeler (2003), and trees were periodically pruned to a height of ≈ 1.5 m. Trees were fertilized semiannually with 30 g per pot of a controlled release fertilizer (Nutricote Total, Type 270,

13N:13P:13K; Chisso-Asahi Fertilizer Co., Tokyo, Japan) and sprayed weekly with an insecticidal soap. On 3 July 2004, three saplings of each chemotype were transferred to a 6 by 4-m screenhouse, randomly placed in 89 by 42 by 15-cm plastic trays, and watered from below as needed. Each tree exhibited a similar architecture, with multiple branches supporting a range of leaf ages.

Psyllid nymphs were obtained from *B. melaleucæ* adults that were collected near Estero, FL. Multiple gravid females were placed in sleeve cages on individual branches that were maintained in an environmental chamber at 25°C and 65% RH, with a L:D photoperiod of 12:12 h (model I-36LLVL; Percival Scientific, Perry, IA; reported error, $\pm 0.5^\circ\text{C}$, $\pm 10\%$ RH). After a 3-d oviposition period, adults were removed, and their eggs were held in the chamber until hatch. The resultant nymphs were used in the experiments.

Experimental Design. The experimental design was a randomized complete block with three factors: chemotype (two), leaf age (two), and herbivory levels (four). Leaves from each chemotype tree were categorized into two age classes: mature and juvenile. Mature leaves were generally darker in color, tougher, and located proximally along stems compared with their juvenile counterparts (Wheeler 2001). Twenty-five leaves of each age class were randomly selected along multiple stems from each of the six *M. quinquenervia* saplings. One mature and one juvenile leaf was randomly selected and excised to obtain a baseline analysis of color, chlorophyll, and tissue percent nitrogen for each age class. The remaining 24 leaves of each age class by chemotype combination were randomly assigned one of four psyllid density treatments: 0 (control), 1, 5, or 10 nymphs/leaf, for a total of six leaves in each treatment. Individual first and second instars were placed on the replicated leaves at preassigned densities on 8 July 2004. After the first cohort completed development, a second inoculation of first and second instars was transferred to leaves on 9 September 2004 in the same manner. All nymphs were transferred using a sable hair brush. Leaf petioles were coated with a sticky-trap material (Tangle-Trap; The Tanglefoot Co., Grand Rapids, MI) to restrict movement of nymphs. Nymphs that became tangled in the sticky barrier or otherwise died were not replaced and recorded infestation levels were adjusted accordingly. Each leaf was monitored on alternate days throughout the study to quantify the number and developmental stage of nymphs as well as to monitor leaf status. Alterations in leaf quality were assessed by removing a randomly selected leaf from each treatment density within both age classes and chemotypes from each tree at biweekly intervals. Sampling events coincided roughly with the third and final instars, respectively. Leaves that abscinded between sampling events were processed and analyzed in the same manner.

Analysis. Herbivore loads were expressed as psyllid feeding days (pfd) per leaf and defined as the cumulative number of nymphs per leaf per day. pfd was calculated by averaging the number of nymphs ob-

served during alternate-day sampling to obtain nymphal densities between sampling dates and summing across all dates. For instance, the number of nymphs tallied on a given leaf during days 1 and 3 was averaged to estimate the nymphal density on that leaf during day 2. pfd for each leaf were categorized into four herbivory levels: 0 feeding days = no herbivory; 1–130 = low; 131–249 = moderate; >250 = high levels of herbivory.

SigmaScan Pro 5.0 (SigmaScan 1999) image analysis software was used to assess alterations in leaf color as a function of foliar damage and total leaf area. The adaxial and abaxial side of each leaf was color scanned (24-bit) at a resolution of 300 dpi with a Hewlett-Packard flat bed scanner (PSC 1210) and saved in bitmap format. These images were processed using macros developed to count the number of pixels that fell within a selected hue and saturation range. Green portions of leaves, which we assume correspond with healthy tissue, were characterized by a hue and saturation range of 55–107 and 15–100, respectively. This healthy tissue color range was identified from the analysis of 30 leaves that exhibited no observable herbivore or pathogen damage from study trees of both chemotypes. Leaf damage assessments were based on the number of pixels that fell outside of the green hue and saturation ranges. After quantifying the number of pixels within the designated ranges, pixel counts were converted to leaf area by using the conversion factor of 1 pixel = 0.0000716845 cm². The ratios of damaged leaf areas to total leaf areas were calculated for both adaxial and abaxial sides and finally averaged per leaf. Each leaf was frozen for preservation after scanning until the chlorophyll was extracted.

To determine the optical density (OD) of chlorophyll in the leaves, we adapted a method of chlorophyll extraction used by Herman (1989). One 6-mm-diameter disk was taken from each of four quadrants of the leaf using a standard hole-punch. These four samples were weighed and placed into a 1.5-ml tube containing 1.0 ml dimethyl sulfoxide (DMSO) to extract the pigment. The tubes were incubated in a dry bath at 65°C for 2 h and allowed to cool for 20 min. Three 0.25-ml subsamples from each tube and four blanks of DMSO were transferred into a flat-bottom, 96-well plate. The plates were read with a spectrophotometer (μ Quant Microplate Spectrophotometer; Bio-Tek Instruments, Winooski, VT) at 660 and 665 nm using a multi-wavelength read by the KCjunior Data Analysis Software (Bio-Tek Instruments). The first wavelength, 660 nm, was chosen in accordance with Herman (1989), who found it to be best for showing levels of herbivore damage for the insect-plant systems of his assay. The second wavelength was selected after a series of spectral scans of healthy *M. quinquenervia* leaves peaked at 665 nm.

The remaining leaf material was dried in an oven at 50°C for a minimum of 1 wk. Each leaf was ground individually with a mortar and pestle and stored in a sealed glass vial in ambient conditions until analysis. The samples were weighed and analyzed for percent

(dry mass) nitrogen using the PE 2400 CHN Analyzer (Perkin Elmer Instruments Norwalk, CT).

Statistics. Three-way analysis of variance (ANOVA) was used to examine the influence of herbivory levels, chemotype, and leaf age on chlorophyll content, percent nitrogen, and percent of leaf tissue that fell outside the healthy range as quantified through color analysis (SAS Institute 1999). Post hoc analyses were conducted with Tukey's honest significant difference (HSD) test. To meet assumptions of normality and homogeneity of variances implicit in the parametric analysis, the arcsine square-root transformation was applied to frequency data before analysis. Analysis of covariance (ANCOVA) was used to assess the influence of herbivory on the degradation rate of chlorophyll, percent nitrogen, and damaged foliar tissue, with sample interval as the covariate (SAS Institute 1999). Foliar damage estimated from spectral scans between mature and juvenile leaves was compared with ANCOVA using herbivory level as a covariate.

The influence of chemotype (chemo), leaf age (age), and herbivory (pfd) on leaf senescence was analyzed with the logistic regression model,

$$\text{logit}(\text{senescence}) = \beta_0 + \beta_1\text{chemo} + \beta_2\text{age} + \beta_3\text{pfd}$$

To test the assumption of linearity, we embedded the preceding model in a larger equation that included quadratic terms to examine departure from linearity (Ramsey and Schafer 2002). Stepwise reduction of all full models was used, removing the least significant ($P > 0.05$) quadratic and highest order interactions first (Ramsey and Schafer 2002). Orthogonal contrasts were used to differentiate the effect of herbivory levels on leaf senescence.

Results and Discussion

Leaves serve as the primary producers of photosynthetic products in most woody plants, and maintenance of these structures is required to supply carbon to meet respiratory needs, as well as to support continued growth, development, and reproduction. This appears especially true for *M. quinquenervia*, which preferentially allocates photosynthate to the production and maintenance of leaves in lieu of reproduction as resources become limiting (Pratt et al. 2005). Maintenance of leaf photosynthetic potential for *M. quinquenervia* is dependent, in part, on the amount of chlorophyll contained within leaf tissues (Kaakeh et al. 1992). In this study, the initial chlorophyll OD (665 nm) of *M. quinquenervia* leaves in the absence of herbivory was 2.49 ± 0.09 (SE) and decreased over time to 2.12 ± 0.27 at the end of the experiment. Surprisingly, there was no difference in chlorophyll between leaf age classes (Table 1), suggesting that both age classes have similar photosynthetic capacity. Similarly, there was no effect of chemotype on chlorophyll OD (Table 1). When pooled across both leaf ages and chemotypes, herbivory by *B. melaleuca* reduced foliar chlorophyll in damaged leaves relative to undamaged leaves ($F = 34.78$, $df = 3, 148$; $P < 0.0001$). In addition, the rate of chlorophyll

Table 1. Herbivory by *B. melaleuca* elicits density-dependent reductions in leaf characteristics of the invasive tree *M. quinquenervia*

	Wavelength ^a		Percent damage	Percent nitrogen
	660	665		
Herbivory level ^b				
None	2.13 (0.06)a	2.25 (0.06)a	13 (2)a	1.5 (0.07)a
Low	1.57 (0.09)b	1.72 (0.10)b	24 (4)a	1.2 (0.02)b
Moderate	0.73 (0.13)c	0.81 (0.14)c	57 (6)b	0.7 (0.05)c
High	0.56 (0.12)c	0.65 (0.13)c	65 (7)b	0.6 (0.05)c
P value	<0.0001	<0.0001	<0.0001	<0.0001
Chemotype				
E-nerolidol	1.51 (0.09)	1.64 (0.10)	35 (4)	1.0 (0.04)
viridiflorol	1.39 (0.10)	1.50 (0.10)	30 (4)	1.0 (0.06)
P value	0.1362	0.0783	0.1919	0.1531
Leaf age				
Mature	1.39 (0.10)	1.64 (0.11)	39 (4)	1.1 (0.05)
Juvenile	1.50 (0.09)	1.48 (0.09)	26 (4)	1.2 (0.06)
P value	0.5082	0.2862	0.0002	0.3626

Means ± SE followed by the same letter within rows are not significantly different at the $P < 0.05$ level (Tukey's HSD).

^a Optical density of chlorophyll in leaves when measured at the wavelengths 665 and 660 nm.

^b Herbivory experienced by each leaf was categorized into four levels: 0 feeding d by *B. melaleuca* = no herbivory; 1–130 = low; 131–249 = moderate; >250 = high.

degradation was accelerated for those leaves experiencing herbivory (ANCOVA, $F = 24.95$; $df = 3,148$; $P < 0.0033$). Increases in the level of herbivory resulted in concomitant decreases in chlorophyll (Table 1), with medium (131–249 pfd) and high (>250 pfd) levels of herbivory reducing chlorophyll content by 64 and 72%, respectively.

Nitrogen content of undamaged *M. quinquenervia* leaves averaged $1.5 \pm 0.07\%$ and ranged from 1.2 to 1.9% (dry mass). These data are consistent with the relatively low foliar nitrogen levels (0.8–2.3%) observed in field populations of this species in Florida (Wheeler 2003). In this study, nitrogen levels for *M. quinquenervia* leaves decreased over time, irrespective of age class, chemotype, or herbivory level, but the rate of nitrogen loss was greater for leaves subjected to herbivory by *B. melaleuca* (ANCOVA, $F = 31.45$; $df = 3,239$; $P < 0.0001$). The amount of herbivory-influenced loss of nitrogen with low, medium, and high levels of feeding resulting in 20, 53, and 60% reductions in nitrogen content, respectively (Table 1).

In contrast to the temporal changes in the previous parameters, the percent of damaged tissue in leaves not subjected to herbivory remained constant over the study period ($F = 0.56$; $df = 3,67$; $P > 0.5$). However, color analysis revealed an increase over time in the amount of damaged foliar tissue on leaves subjected to sustained *B. melaleuca* feeding (Table 1). As before, increases in herbivory levels resulted in increases in the amount of damaged leaf area ($F = 11.25$; $df = 3,148$; $P < 0.0001$). Leaves sustaining moderate to high levels of herbivory often progressed from dark green to yellow and finally light tan as they deteriorated, often abscising during the two latter color phases. These changes in color, particularly the yellowing phase, were often more pronounced along the main leaf veins and vascular tissues. In contrast to chlorophyll content, younger leaves exhibited less color change when attacked by the herbivore than their older counterparts (ANCOVA, $F = 5.46$; $df = 1,148$; $P = 0.0209$). One

explanation for this may be that younger leaves remain green longer than mature leaves when experiencing similar herbivory loads because they receive soluble forms of nitrogen translocated from older leaves (Thomas and Stoddart 1980).

Leaf senescence is characterized by chlorophyll breakdown, cessation of photosynthesis, and ultimately abscission (Thomas and Stoddart 1980). Herein, only herbivory (pfd) induced premature senescence of *M. quinquenervia* leaves ($\chi^2 = 62.0$, $P < 0.001$; Fig. 1), and the fit of a reduced logistic regression model to these data gives:

$$\text{logit}(\text{abscission}) = -5.8405 + 1.5669 \text{ pfd}$$

Feeding by *B. melaleuca* increased the odds of leaf abscission by 4.7 times compared with leaves that were not subjected to herbivory (95% Wald confidence interval: 3.0–7.6). However, neither leaf age ($\chi^2_1 = 0.53$, $P < 0.4683$) nor chemotype ($\chi^2_1 = 1.99$, $P < 0.1577$) influenced the likelihood of abscission. The similarity in responses among young and old leaves is surprising when considering that preliminary field-based observations and experimental evidence suggest differential susceptibility to feeding by *B. melaleuca*. One explanation for the disparity between the predicted and realized interaction of herbivory and leaf age on abscission may be that young leaves matured during the course of the study and thereby senesced in response to herbivory as mature leaves. Alternatively, leaf age categories may have been too narrowly defined as they excluded the smallest leaves near the meristematic bud.

Under the assumptions of foraging theory, herbivores would be predicted to exploit host tissues with the greatest concentrations of limiting or essential nutrients (Begon et al. 1996). Therefore, it is not surprising that most psyllids, including *B. melaleuca*, are often flush-feeders, intercepting the inflow of highly concentrated nutrients along the main delivery channels to growing leaves (White 1993). In addition, psyllids are known to manipulate their host plant's

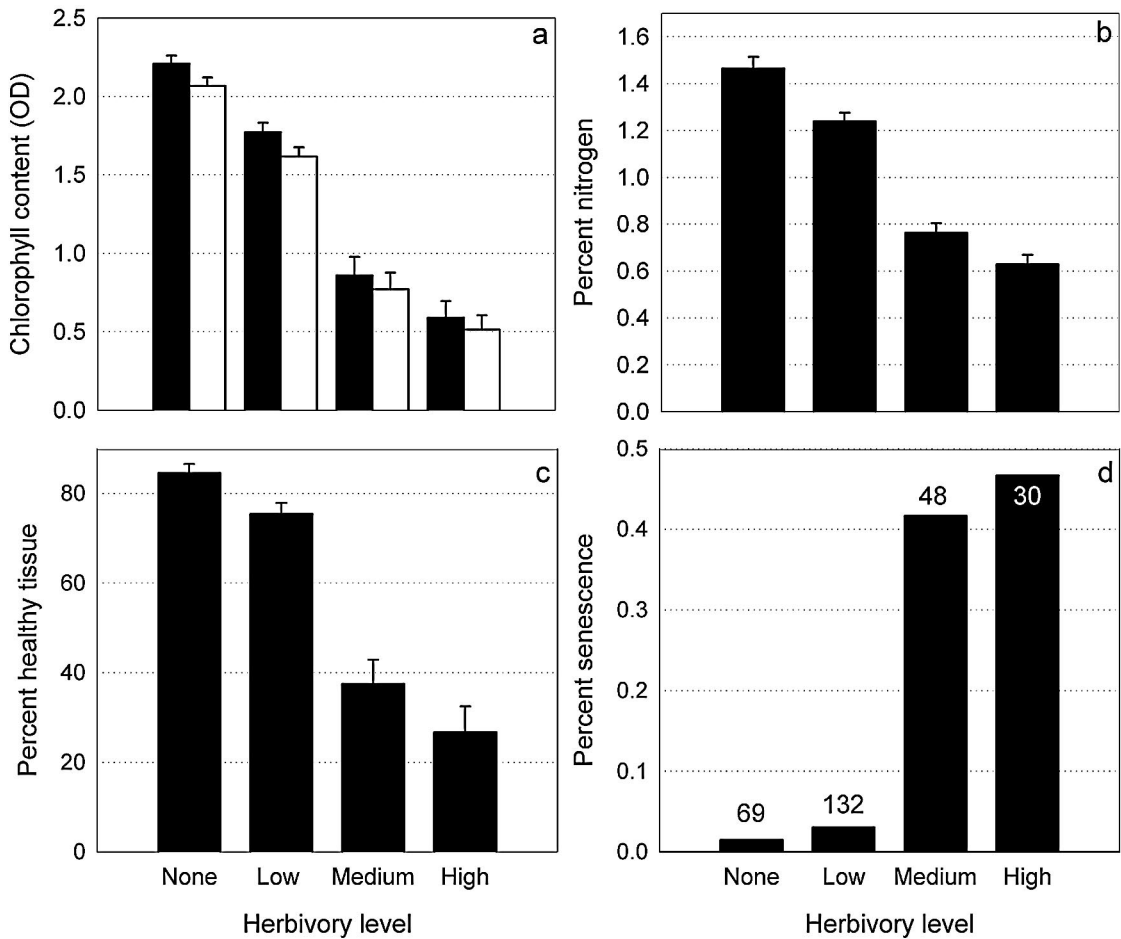


Fig. 1. Herbivory by *B. melaleuca* results in density-dependent reductions in foliar chlorophyll content, percent nitrogen, spectral signatures, and leaf senescence of healthy tissue (\pm SE) of the invasive tree *M. quinquenervia*. Low, medium, and high levels of herbivory correspond to: 0 psyllid feeding days = no herbivory; 1–130 = low; 130–249 = moderate; >250 = high. Black and white bars in figure a represent chlorophyll content measured at 665 and 660 nm, respectively. Numbers above bars in d represent sample size.

physiology to prolong and concentrate the availability of nitrogen. As suggested by White (1993) for *Cardiaspina densitexta* Taylor, feeding by *B. melaleuca* may induce tissue breakdown in the mesophyll cellular layer, a mechanism by which psyllids ameliorate their food source by augmenting normal phloem translocates. This method of senescence feeding hastens the rate of senescence of the leaf tissues surrounding the feeding site to increase the rate of delivery of nutrients into the phloem where it feeds (Thomas and Stoddart 1980, White 1993). This increase in the rate of senescence, often attributed to an injection of a phytotoxic saliva, becomes considerably more apparent during the later instars (Hodkinson 1974). In some cases, after the saliva enters the plant's vascular system, it can spread to other parts of the plant (Hodkinson 1988). In the course of this study, we observed that the increased rate of leaf senescence was not localized to individually damaged leaves. In a few cases, for instance, herbivore-free leaves abscised that were ad-

jacent to leaves subjected to high densities of *B. melaleuca*.

Melaleuca quinquenervia leaves, like many evergreen species, are long-lived with a life span of ≈ 4 yr (Van et al. 2002). A prolonged leaf life span and low tissue nutrient concentrations may enable evergreen species to reduce nutrient loss, as an alternative to using a high rate of nutrient translocation from senescing leaves (Aerts 1996). Experimental evidence has shown that plants can mitigate the impacts of herbivores by increasing leaf longevity after bouts of herbivory (Hodkinson 1974). If extending leaf longevity is *M. quinquenervia*'s primary compensatory defense against attack of younger buds and leaves, the increased rate of senescence of older leaves caused by psyllid feeding has strong implications for the decrease in fitness of the tree.

Herein, we quantified impacts of herbivory on expanded leaves of variable ages. However, *B. melaleuca* also exploits the small and compressed leaves of

flushing buds. This brings *B. melaleuca* into contact with another biological control agent, the *Melaleuca* weevil *O. vitiosa* (Center et al. 2000, Pratt et al. 2002, 2005). Adult weevils feed indiscriminately and superficially on *M. quinquenervia* foliage, whereas larvae are specialized flush-feeders, consuming only the newly developed, expanding leaves at branch apices (Purcell and Balciunas 1994, Pratt et al. 2005). Competitive interactions among these herbivores on seedlings seem independent rather than antagonistic or synergistic (Franks et al. 2005). Within-plant feeding specialization, however, may influence herbivore interactions on a larger spatial scale. Unlike *O. vitiosa* larvae, *B. melaleuca* nymphs and adults readily exploit older, tougher, fully expanded leaves that occur lower in the canopy. Therefore, one may hypothesize that broader feeding niches permit continued psyllid population increase, whereas the more specialized *O. vitiosa* is limited to ephemeral flushes of leaves (Pratt et al. 2004a). Future research will focus on the population dynamics and competitive interactions of these species over larger spatial and temporal scales.

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